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Operant Conditioning in the Garter Snake (Thamnophis)

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OPERANT CONDITIONING IN THE GARTER SNAKE (THAMNOPHIS)

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BY

William A. Schmitz

B. S., Eastern Illinois University, 1968

THESIS

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I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING
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OPERANT CONDITIONING IN THE GARTER SNAKE (*THAMNOPHIS*)

BY

WILLIAM A. SCHMITZ

B. S. in Zoology, Eastern Illinois University, 1968

ABSTRACT OF A THESIS

Submitted in partial fulfillment of the requirements
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ABSTRACT

Ten garter snakes were tested for runway acquisition, correct turn response in a simple T-maze, or both, for food reinforcement. Seven of seven subjects met criterion for learning to run a 23 inch long alleyway. Mean latency times showed a general decrease over a 23 day period. Five of nine subjects met criterion for learning a correct turn response in a simple T-maze. Subjects mastering the task required from 14-157 trials. One of two subjects met criterion for learning the reverse response of the T-maze exercise, requiring 35 trials. Results are similar to those previously reported for reptiles and other non-primate vertebrates.

The undersigned, appointed by the Head of the Department of Zoology,

have examined a thesis entitled

Operant Conditioning in the Garter Snake (Thamnophis)

Presented by

William A. Schmitz

a candidate for the degree of Master of Science

and hereby certify that in their opinion it is acceptable.

ACKNOWLEDGEMENTS

The advice and guidance of Dr. Michael A. Goodrich, my faculty adviser, was helpful at every stage of research and writing. The training which I received as a pupil in Dr. Goodrich's classes led me to further pursue study in Ethology; and discussions, both brief and lengthy, with him provided me with helpful direction and a fuller understanding concerning my research.

Thanks are also given to Dr. E. O. Moll and Dr. F. R. Schram, members of the Graduate Faculty, for helpful comments made upon reading a manuscript of the thesis.

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INTRODUCTION

Our knowledge of evolutionary development prompts us to examine the possibility of ranking all groups of animals on the basis of their learning capacities. Each taxon must then be studied in this regard to verify its theoretical rank. Only a small amount of study has been done on learning in the Suborder Serpentes and the Class Reptilia in general.

Reptiles other than snakes have been conditioned to move down runways or make two-choice discriminations in a number of experiments. R. M. Yerkes (1901) demonstrated operant conditioning in a single specimen of the spotted turtle (Clemmys guttata) by measuring its ability to run two labyrinths of increasing difficulty. D. B. Casteel (1911) conducted a series of two-choice discrimination experiments to show the ability of Chrysemys picta marginata, the midland painted turtle, to respond to patterns of different form, black and white, and line width and direction. In 1963, P. van Sommers established lever-pressing as a conditioned response for access to air in Pseudemys scripta elegans, the red-eared turtle. Running time measurement was part of a study by Spigel (1965) with Chrysemys picta marginata in which a runway was employed in conjunction with a two-choice brightness discrimination chamber. Morlock, Brothers, and Shaffer (1968) tested Chrysemys picta picta, the eastern painted turtle, in a simple E-shaped maze and demonstrated acquisition of correct turn response.

Lizards have been subjects for a considerable number of operant conditioning experiments. Brightness discrimination by Crotaphytus collaris,

the collared lizard, was studied by Vance, Richardson, and Goodrich (1964). Alkov and Crawford (1965) demonstrated runway acquisition by Iguana iguana. In 1968, Krekorian, Vance, and Richardson conducted two-choice discrimination experiments with twenty Dipsosaurus dorsalis (desert iguanas) to show the importance of body temperature as a factor of learning. Julian and Richardson (1969) conditioned six Dipsosaurus dorsalis on each of three mazes to show the relationship between temperature and learning. Kemp (1969) measured the lever-pressing response in Dipsosaurus dorsalis.

The caiman has been used in at least one learning study (Williams and Robertson, 1970). Discriminative ability of the subjects was demonstrated by use of brightness cues in a T-maze.

The earliest study of operant conditioning in snakes was that of W. N. Kellogg and W. B. Pomeroy (1936). Twelve water snakes (Natrix sipedon) were tested for two-choice discrimination in a multiple T-maze. Individual performances varied greatly, and the group as a whole did not meet the predetermined criterion.

D. L. Wolfle and C. S. Brown (1940) attempted to improve on Kellogg and Pomeroy's study, but the data they collected was no more conclusive. Their subjects, Natrix rhombifera rhombifera, did not become conditioned to either a multiple T-maze or a two-chamber electric shock apparatus.

In 1966, F. T. Crawford and C. W. Bartlett investigated runway learning in Elaphe obsoleta spiloides, the gray rat snake. Although their experimental group showed better results than their control group, no positive conclusions were made.

Crawford and Holmes (1966) obtained better results from four Elaphe obsoleta quadrivittata (yellow rat snakes) and two Elaphe

obsoleta rossalleni (Everglades rat snakes). The subjects were conditioned to escape vibration in a two-chamber apparatus. Data from fifty trials per subject indicated highly variable individual behavior, but a decrease in average response time for the group.

METHODS

1. Subjects

Nine adult Thamnophis sirtalis sirtalis, the eastern garter snake, and one Thamnophis radix, the plains garter snake, were used in this study. T. sirtalis, although ranging over all of the eastern United States and common throughout much of its range, has not previously been studied for learning. This neglect has most likely been due to the generally negative disposition of garter snakes when in the presence of man. In addition to their relative abundance, captive Thamnophis were observed to be more active and feed more frequently than other snakes, the latter feature desireable because of its direct relationship to the rate of testing when food is used as a reinforcement. Subjects had been in captivity at least nineteen days and as long as seventeen months prior to testing, and data concerning feeding and shedding was recorded for each subject from date of capture. The total lengths of the T. sirtalis subjects ranged from 53-85 cm., and the total length of the T. radix was about 60 cm. (see Table 1)

Subjects were housed in two batteries of wood cages, with five cages in each set. Each cage was 11½ in. long, 7 in. wide, and 11½ in. high (inside dimensions), and each was equipped with a sliding glass door. The room in which the subjects were both maintained and tested was 10 ft. by 10 ft. and had one large window area through which daylight was allowed. Two long flourescent bulbs (40 w. each) were located above the testing apparatus in the center of the room. The temperature of the

Table 1. Sex, total length, capture data, and length of habituation period of subjects (*Thamnophis sirtalis* and *T. radix*)

Subject	Sex	Total length (cm.)	Date and location of capture	Length of habituation period (days)
1		68	prior to May 1970 Coles Co., Illinois	110
2[1]		60[2]	Spring 1971	110
3	0	76	19 Jun 1971 Coles Co., Illinois	81
4	0	53	20 Jun 1971 Coles Co., Illinois	110
5	0	69	3 Jul 1971 Union Co., Illinois	71
6	0	77	4 Jul 1971 Union Co., Illinois	95
7	0	85	23 Jul 1971 Coles Co., Illinois	77
8	0	68	28 Aug 1971 Coles Co., Illinois	38
9	0	68	28 Sep 1971 Coles Co., Illinois	10
10	0	55	12 Dec 1971 Coles Co., Illinois	4

[1] *T. radix* [2] an estimate length

room was maintained between 75-80 F. Human activity within the room was limited to periods when the subjects were being fed or tested.

2. Motivation

Much of the difficulty in measuring learning in reptiles has been in finding an appropriate means of motivation. Temperature of the environment has been employed as motivation for both lizards (Alkov and Crawford, 1965; Vance, et al., 1965; Kemp, 1969) and snakes (Kellogg and Pomeroy, 1936; Wolfle and Brown, 1940). The aquatic habits of freshwater turtles have prompted the use of access to air (van Sommers, 1963; Morlock, et al., 1968) and access to water (Spigel, 1965) as reinforcements. Electric shock has been used as negative reinforcement for lizards (Vance, et al., 1965), turtles (Casteel, 1911), caimans (Williams and Robertson, 1970) and snakes (Wolfle and Brown, 1940). An attempt at using a vibratory floor to elicit a response in snakes was made by Crawford and Holmes (1966).

Food and water reinforcements, so often used in bird and mammal learning studies, have generally been considered inappropriate for reptile experiments. Kellogg and Pomeroy (1936) stated "Food was obviously out of the question as an incentive for organisms which eat as irregularly as snakes". There may be some truth to this when applied to some species; however, in a runway study with Elaphe obsoleta spiloides, Crawford and Bartlett (1966) demonstrated the possibility of using food as a reinforcement for snakes. Positive reinforcement such as this was felt to be more desireable than negative reinforcement for the present study. Because of the nature of a rat snakes food, i.e.small mammals, the rate of testing in Crawford and Bartlett's study was limited by the appetite of the subjects. It was believed that garter snakes could be condi-

tioned to eat small portions of food, thus making it possible to test the subjects as often as several times per day, if desired.

According to C. C. Carpenter (1955), the diet of the common garter snake is varied. Although no food preference has been determined, the principle food taken by the common garter snake is earthworms, followed in decreasing order of importance by frogs, toads, salamanders, fish, leeches, small mammals, birds, caterpillars, and perhaps other insects. Earthworms were suitable reinforcement for this study for the following reasons: 1) they are a major part of the garter snake's diet in the wild, 2) they could be procured year-round with little effort, and 3) they could be broken into smaller pieces and still be accepted as food by the subjects.

3. Habituation Period

Prior to testing, each subject underwent a period of habituation ranging from four to 110 days (Table 1). The habituation period had several purposes: 1) it indicated the suitability of each snake for study, based on how readily it ate, 2) it aided the investigator in determining the amount of food which both fills the nutritional needs of the snake and leaves the snake active and willing to eat more, and 3) it habituated the subjects to the presence of the investigator and to the conditions of their captivity. The equivalent of one earthworm (10-15 cm. long) was fed to each subject every other day during the period of habituation. Water was available to the subjects at all times.

4. Straight Runway Experiment

a. Apparatus

Subjects were run in a 23 in. long alleyway, which was 7½ in. wide

and 11 in. high. The goal box was 11 in. long, 7½ in. wide, and 11 in. high. (Inside dimensions in each case.) The subjects' normal cages doubled as starting boxes. The alleyway and goal box were constructed of unpainted pine lumber and covered with glass. The glass covering the alleyway was removable, but that on the goal box was permanent. (see Fig. 1.) A strip of ½ in. high wood was glued across the width of the goal box floor. This strip of wood prevented the subjects from seeing the piece of worm until the subject had entered the goal box.

b. Procedure

Seven Thamnophis sirtalis sirtalis and one Thamnophis radix were tested once each day for 23 days. For convenience of referral, subjects were numbered consecutively based on the date of capture. Subjects were tested only during daylight hours, and the artificial light located above the apparatus was on only during testing sessions. Subjects were allowed to eat only on completion of the runway; however, water was available in their cages at all times. If a subject was in an opaque condition, testing of that individual was discontinued until it had shed.

The sensitivity of certain reptiles to distractions is a factor which had to be considered. In previous studies, investigators have positioned themselves behind one-way screens (Casteel, 1911; Kellogg and Pomeroy, 1936; and Vance, et al., 1965) or have relied on photocells and chronometers (Crawford and Bartlett, 1966). The use of photocells does not take into account the tendency for a snake to extend its head and then draw it back again. Rather than sitting behind a one-way screen, the movement of the subjects in this experiment was viewed through the cracks between the cage and the alleyway and between the alleyway and the goal box. While viewing in this manner, the observer remained seated motionless.

Fig. 1. Unpainted straight runway apparatus.

Prior to each run, a piece of earthworm approximately 4-5 cm. long was placed toward the rear of the goal box. The alleyway was then moved in front of a cage door. The door of the cage was raised slowly, allowing it to vibrate slightly while going up. It had been observed that, at times, subjects appeared to be "dozing". By slightly vibrating the door, it was hoped that the subject would be further aware of the presence of the testing apparatus.

The following times were recorded for each run:

1) latency time - time between opening the cage door and the subject's head entering the alleyway.
2) running time - time between subject's head entering the alleyway and the subject's head entering the goal box.

If a subject did not enter the alleyway within ten minutes after the cage door was lifted, no further attempt was made until the next session. Kellogg and Pomeroy (1936) had demonstrated that when both "head" and "tail" times were recorded for each trial, the difference between the two times remained quite constant. Crawford and Bartlett (1966) did not express any difficulty with their use of "head" times in measuring runway acquisition. The variation in lengths of subjects and the limited size of the testing apparatus further influenced the use of the subject's head as the basis for times in the present study. Times were taken using the sweep second hand of a wristwatch, so are recorded only to the nearest five seconds.

After a subject had completed the runway and had eaten the piece of worm, it was gently prodded back to its cage with a wooden yardstick, or in some cases allowed to return on its own.

Criterion for learning was set at four out of five consecutive

latency times of less than 100 seconds and four out of five consecutive running times of less than 100 seconds.

5. Second Runway Experiment

As a preliminary exercise to the T-maze experiment, eight subjects were tested in a straight runway under different conditions than the runway experiment described above. The same runway apparatus was painted flat black, both inside and out (Fig. 2). It was hoped that this might make the apparatus appear more uniform - a factor which would be important in the T-maze experiment. Possible decreased activity had been observed in several subjects near the end of November, possibly related to the shortening of daylight hours. For this reason, another condition was altered at this time - the artificial lights were left on 24 hours per day. In an attempt to increase the number of trials run during the period of the study, the subjects were tested twice each day for five days under these conditions. Criterion for acquisition of the response of running this alleyway was set at three out of four consecutive latency times of less than 100 seconds and three out of four consecutive running times of less than 100 seconds.

6. T-maze Experiment

a. Apparatus

The same alleyway that was used in the runway experiments served as the initial segment of the T-maze. The cross of the T was 24 in. long, 7½ in. wide, and 11 in. high. A goal box 12 in. long, 7½ in. wide, and 11 in. high was at each end of the cross piece. The entire apparatus was constructed of pine lumber, painted flat black, and covered with

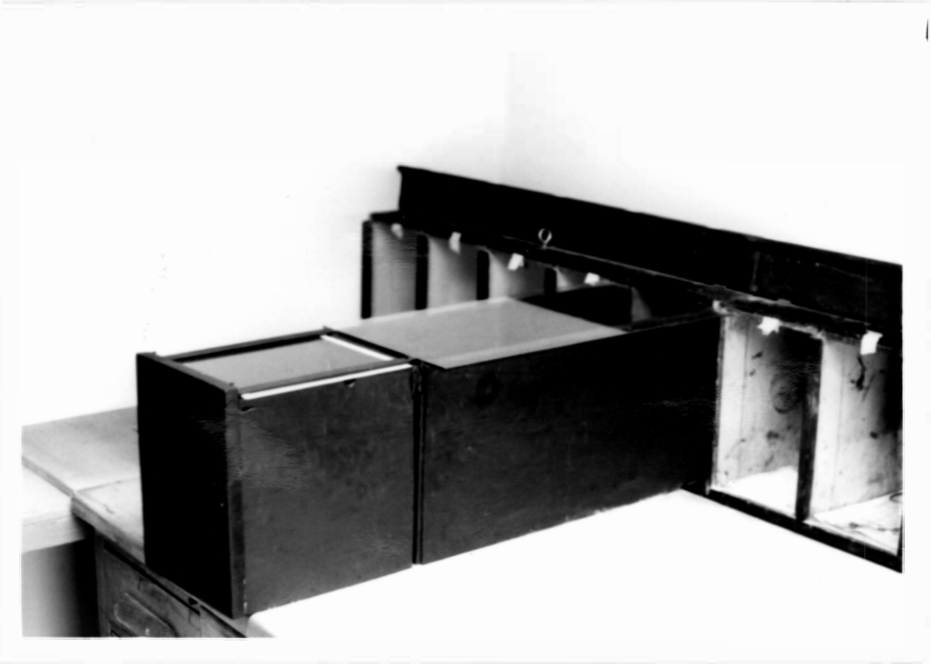


Fig. 2. Painted straight runway apparatus.

glass. A strip of ½ in. high wood was glued across the width of each goal box floor. One small mirror was placed above the subject's cage to allow a view of the end of the runway segment. Two additional mirrors were placed on the cross of the T to allow a view of the entrances to each goal box. (Figs. 3 and 4.)

b. Procedure

Nine T. sirtalis sirtalis were tested in the T-maze apparatus. Before each trial, a piece of food was placed behind the strip of wood in the goal box to the subject's right. For the first 35 trials, a piece of earthworm 15-25 mm. long was used as reinforcement. The deaths of two subjects prompted an increase in the size of earthworm to 30-40 mm. beginning with the 36th trial. For a sixteen day period (trials 100-115) during February, earthworms could not be obtained, so pieces of raw hamburger were substituted. As suggested by Casteel (1911), odor of the food reinforcement might be a factor in reptile discrimination studies. At the beginning of each session, a piece of food was rubbed on the floor of the incorrect goal box. The subject's cage was positioned in front of the entrance to the maze, and the cage door was lifted in the same manner as described in the runway experiment. Movement of the subject from its cage into the maze was viewed through a crack at that point. After the head had entered the alleyway, the investigator sat directly opposite the maze, so that the subject could be seen in the mirror system (Fig. 4). The general path followed by each subject while entering one or the other branch of the T was recorded as to whether the subject went around the corner, around the middle, to the end wall, or across from one side to the other (Fig. 5).

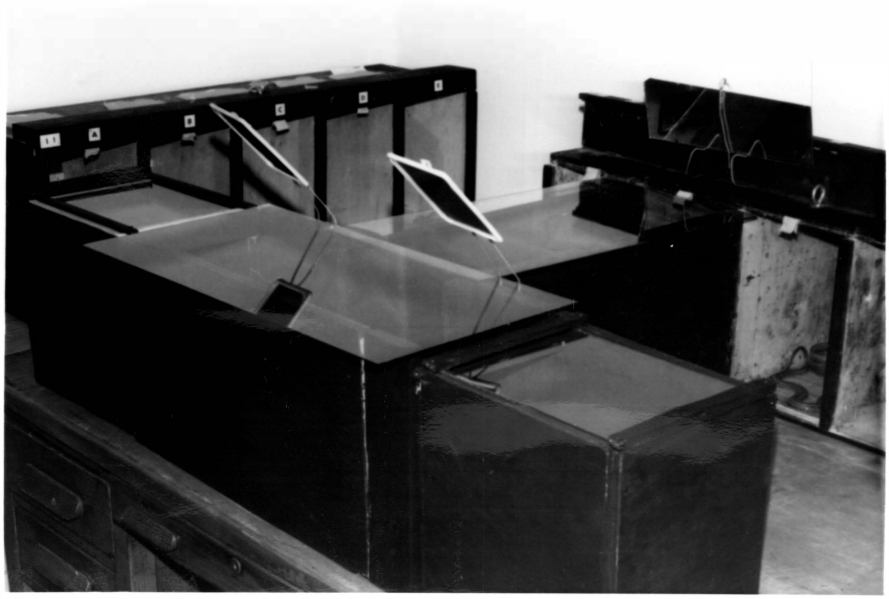


Fig. 3. T-maze apparatus.

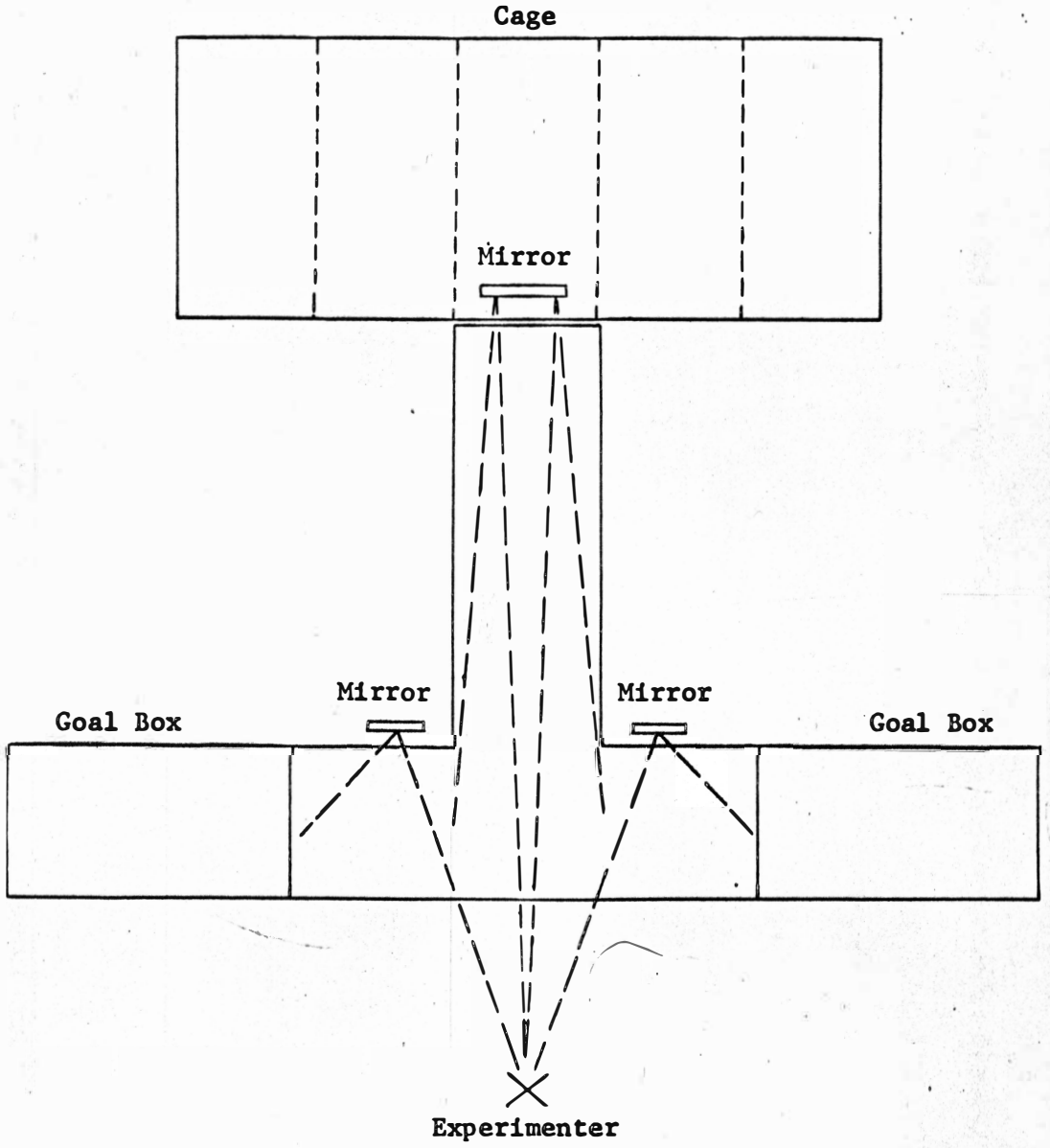


Fig. 4. Arrangement of T-maze apparatus with mirror system.

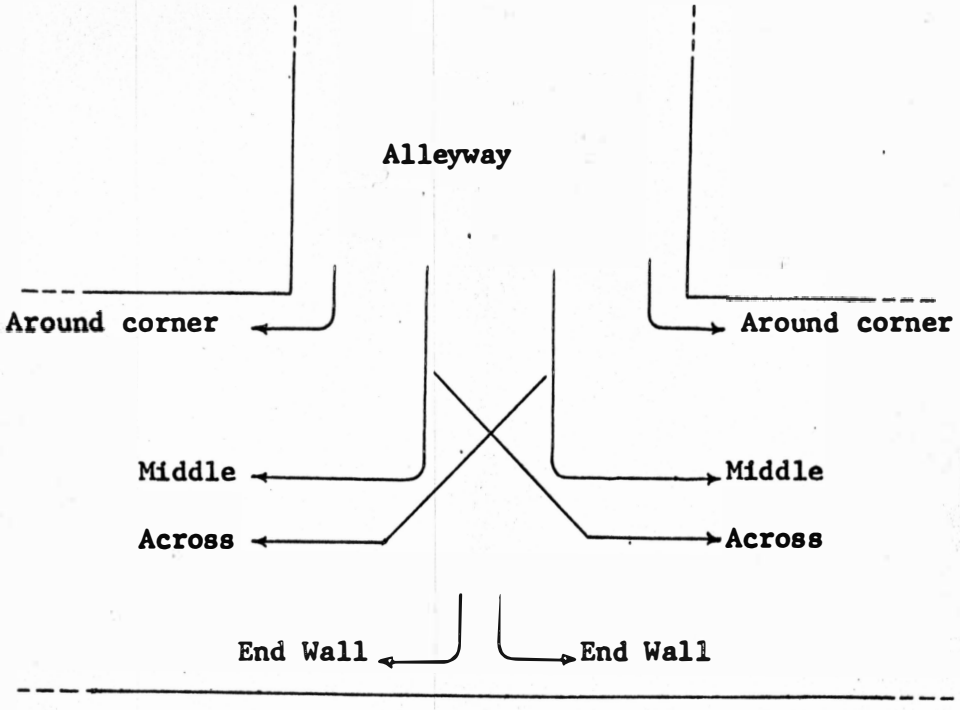


Fig. 5. Diagram of T-section showing general paths taken by subjects.

For the first 94 trials, a "correction" method was employed, whereby, if a subject initially made the incorrect choice, it was allowed to continue the trial until the correct choice was made and reinforced, and then was prodded back to its cage with a wooden yardstick. Beginning with trial 95, a "non-correction" method was used, allowing the subject only one choice per trial and reinforcement only for a correct choice.

Subjects were generally tested twice each day on the first 38 days and once each day on the next 97 days. For both the "correction" and "non-correction" methods, an error was recorded if the subject's head entered the incorrect goal box. Criterion for learning the T-maze exercise was set at eleven correct choices out of twelve trials, with at least the last eight consecutive trials correct.

A stopwatch was used to measure the following times to the nearest one second:

1) latency time - time between opening the cage door and the subject's head entering the maze.
2) running time - time between the subject's head entering the maze and the subject's head entering a goal box.

A latency time of more than ten minutes resulted in the postponement of that trial until the next session. Testing of a subject in an opaque condition was discontinued until that individual had shed.

7. T-maze Reversal Experiment

Two subjects were tested in the apparatus described in the T-maze experiment and under the same general conditions. Each of the subjects investigated for reversal learning had previously reached criterion in the initial T-maze study.

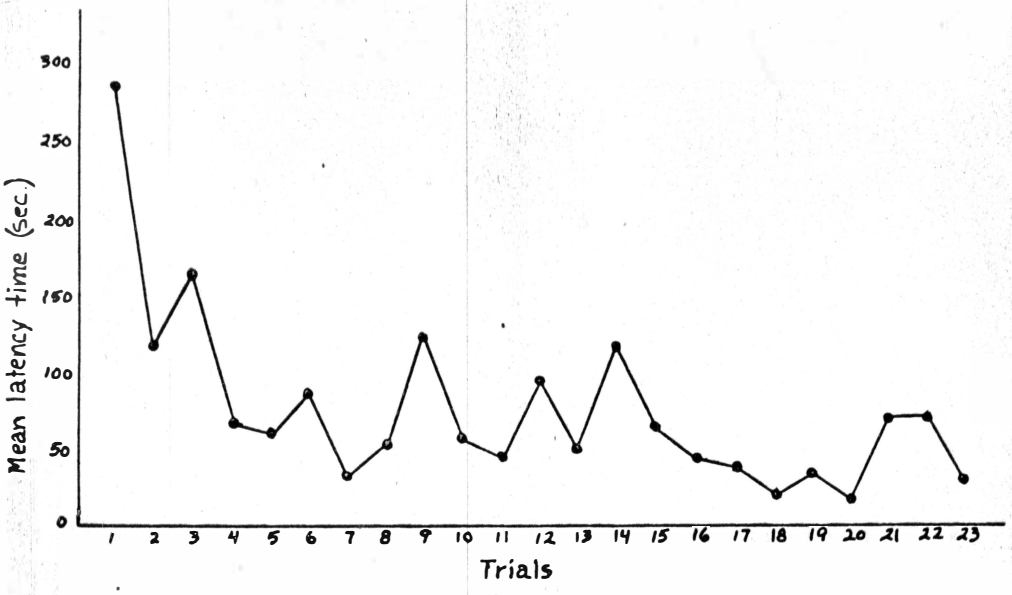


Fig. 6. Mean latency times of seven subjects for first 23 days of straight runway experiment.

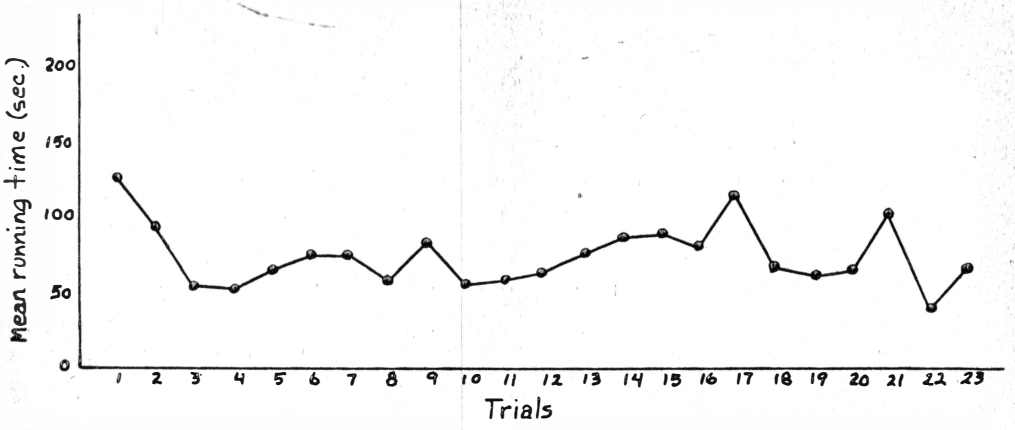
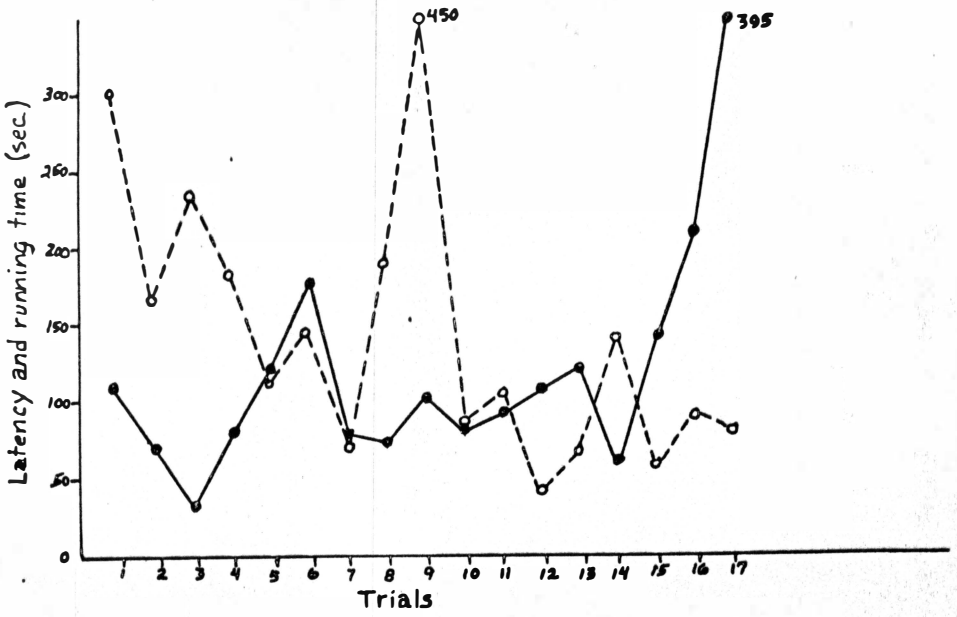


Fig. 7. Mean running times of seven subjects for first 23 days of straight runway experiment.

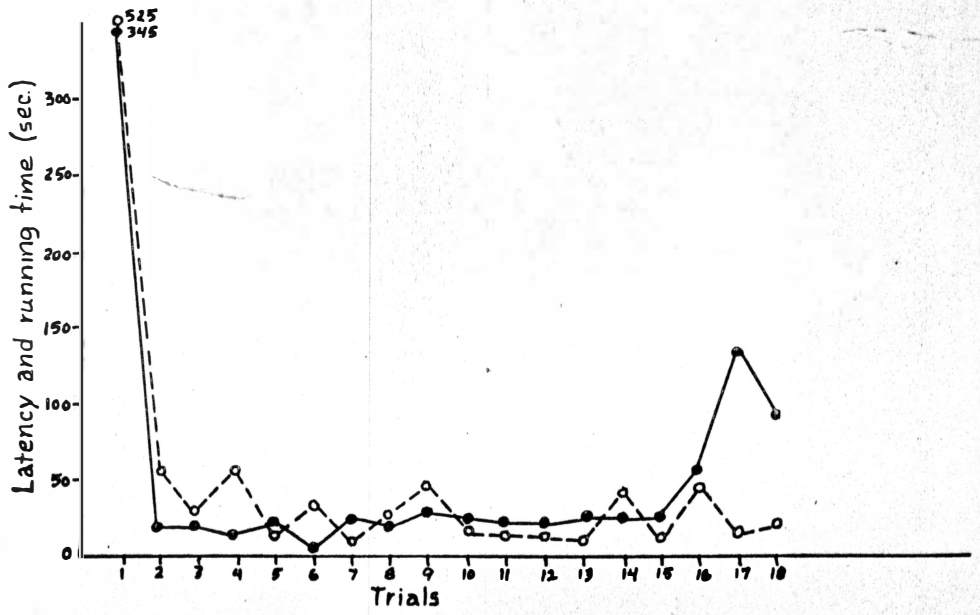
Fig. 8. Individual latency and running times of seven subjects for the first 23 days of the straight runway experiment. (pp 21-23).

o- - - -o latency times

●———● running times



Subject 1



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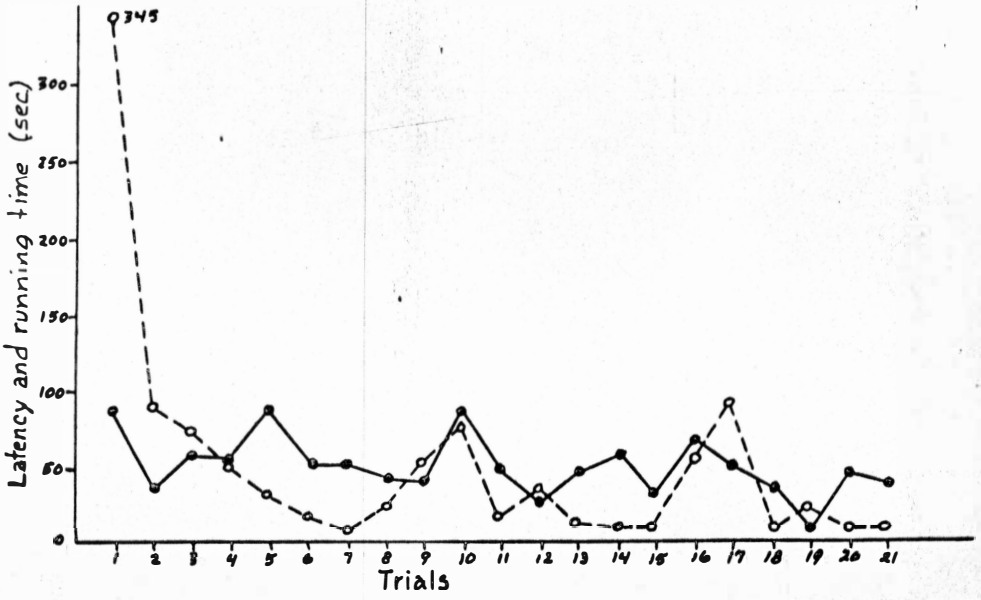

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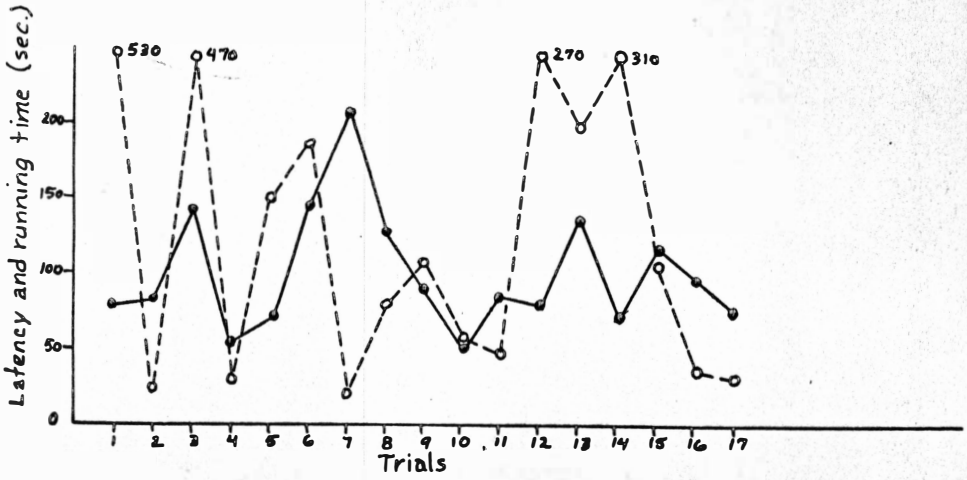

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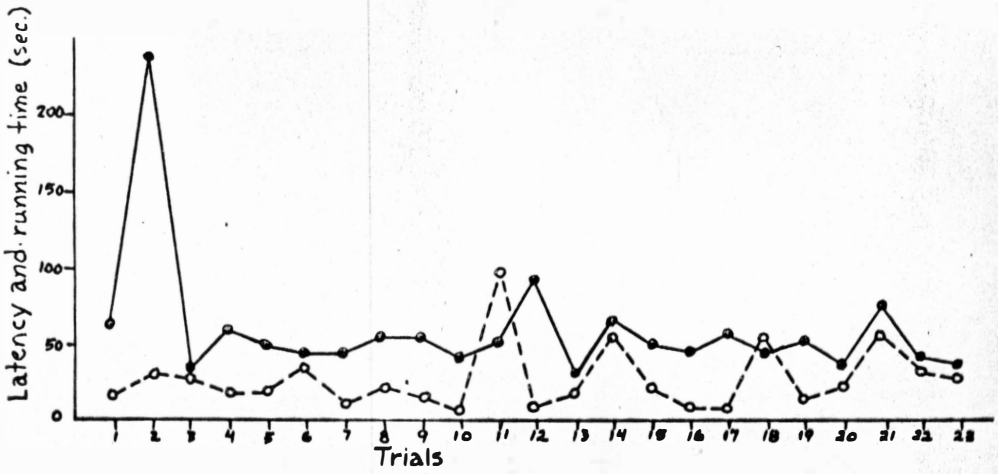

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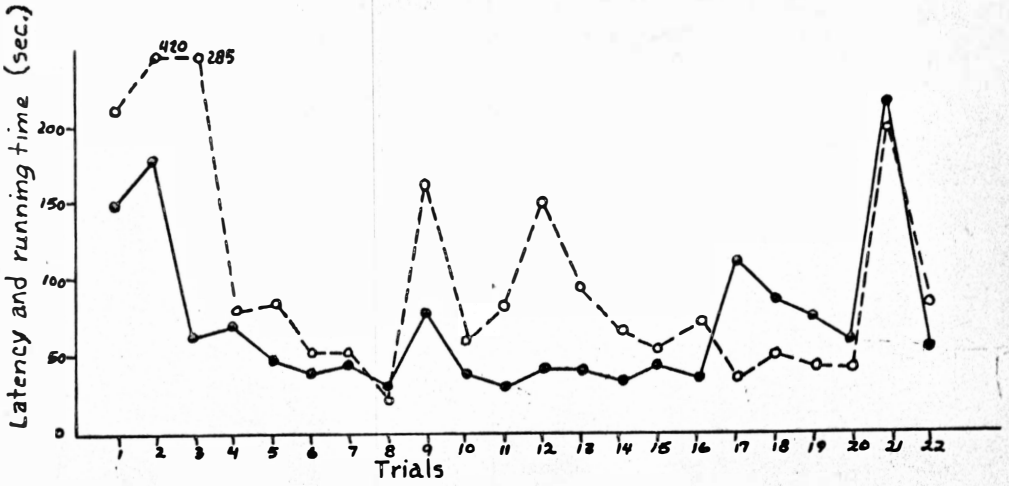

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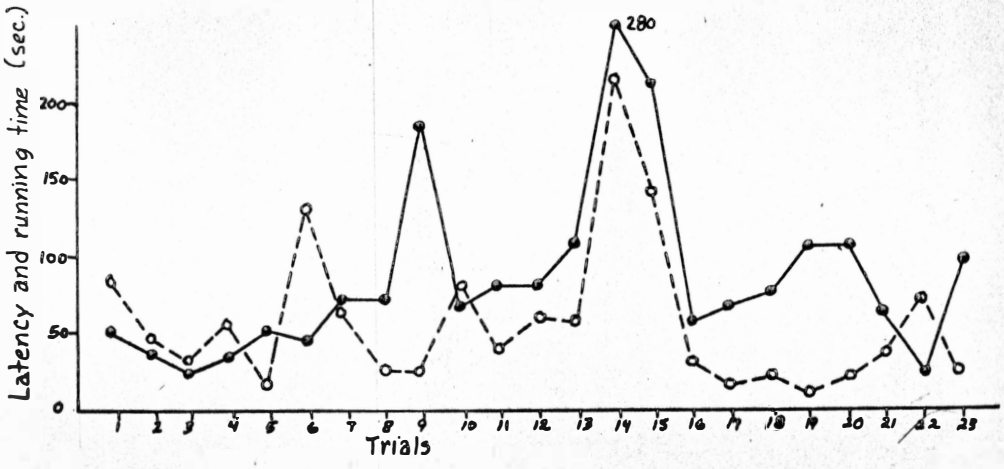

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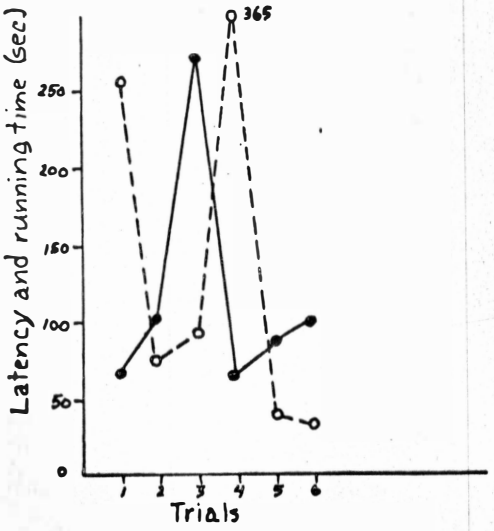
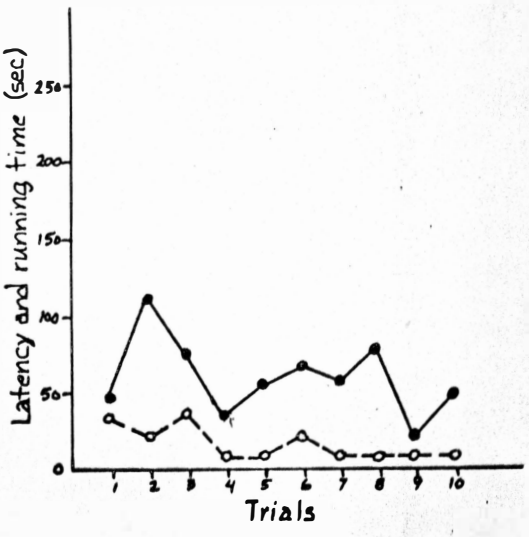


Subject 2



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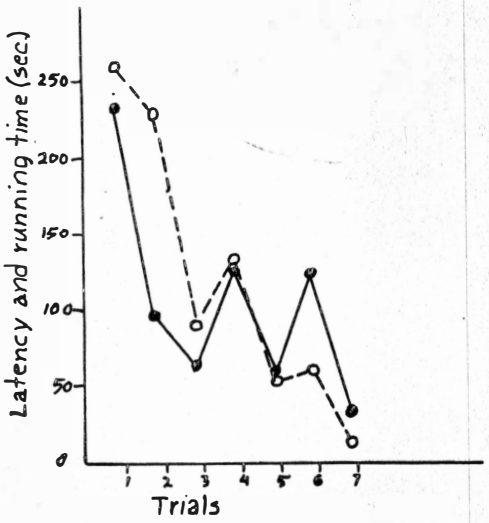

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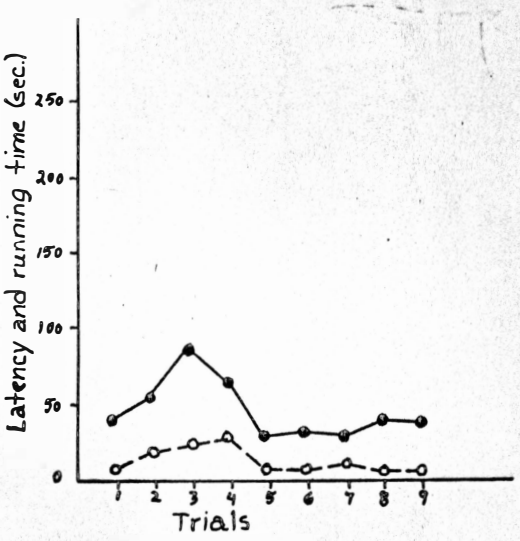
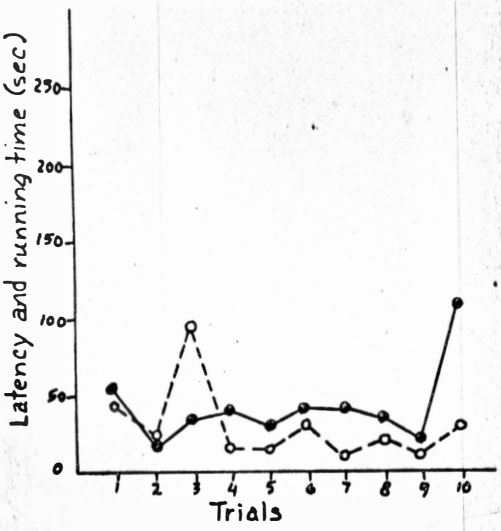


Subject 5



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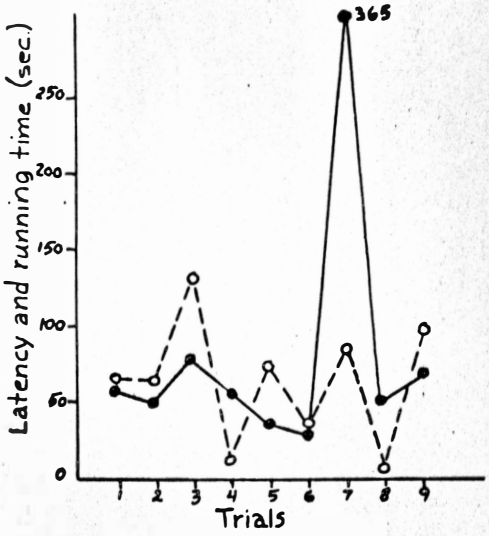
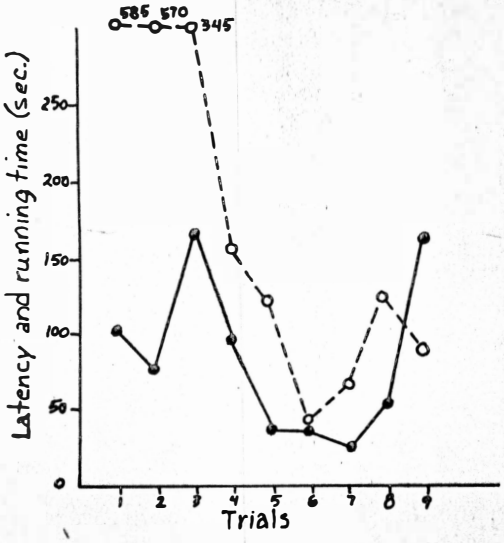


Subject 8



Subject 9

in the previous runway experiment. None of the subjects shed during this five day period.

3. T-maze Experiment

Five out of nine subjects reached criterion for learning the T-maze. The number of trials required before acquisition of criterion by Subjects 1, 4, 5, 7, and 9 and the total number of trials run by each of the nine subjects are given in table 2. Subjects 1, 3, and 6 died of unknown causes after 30, 35, and 34 trials respectively. Subject 8 had not met criterion after 169 trials. Rate of learning the T-maze, based on correct turns, is presented in fig. 10.

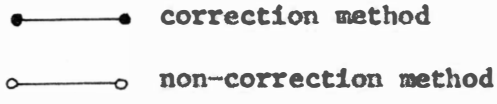
For the first 75 days of the T-maze experiment, the subjects were run twice each day. The percentages of correct responses of the total for each of nine subjects are shown in table 3 for the first trials of each day and the second trials of each day. Eight of the nine subjects had a higher percentage of correct responses on first trials than on second trials. The difference between group results of the first trials and second trials was highly significant (x^2 test $P<0.01$), so the change to one trial per day was made. Correct responses were made in at least 60% of the total trials for each of the subjects when tested once each day.

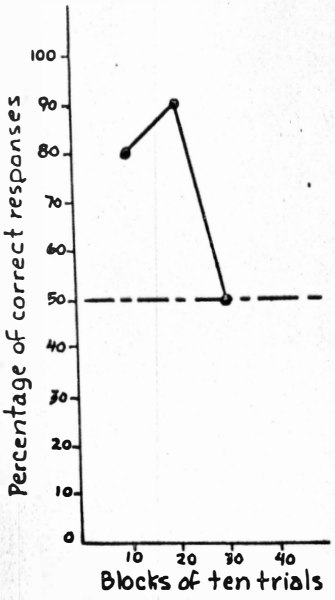
Latency times for each trial are not presented, because they tended to be quite uniform for each subject. Subject 4 generally had the highest latency times, frequently with times over 100 seconds. Subject 5 had an average latency time of less than ten seconds, and times of three seconds or less were common for Subject 5. Latency times for the remaining subjects generally ranged under 60 seconds.

Table 2. Total number of trials and trials required to reach criterion in the T-maze experiment

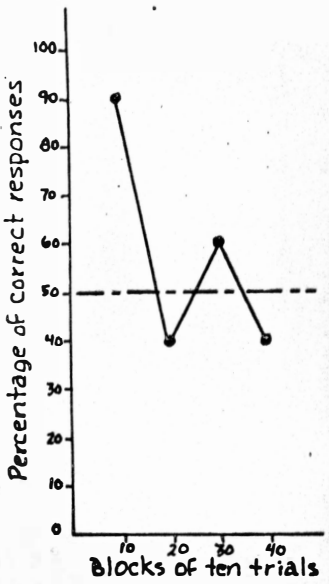
Subject	Total number of trials given	Number of trials required to reach criterion
1	30	15
3	35	-
4	86	16
5	157	157
6	34	-
7	116	112
8	169	-
9	153	14
10	120	-

Fig. 10. Percentage of correct responses in blocks of ten trials by nine subjects in T-maze experiment. (pp 28-31)





Subject 1



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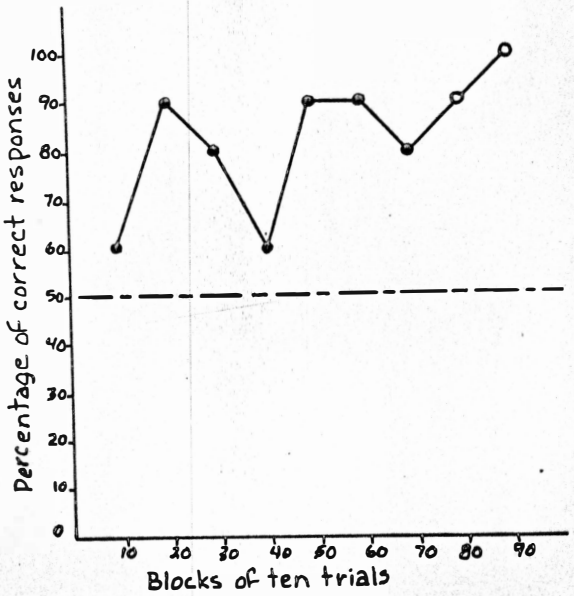
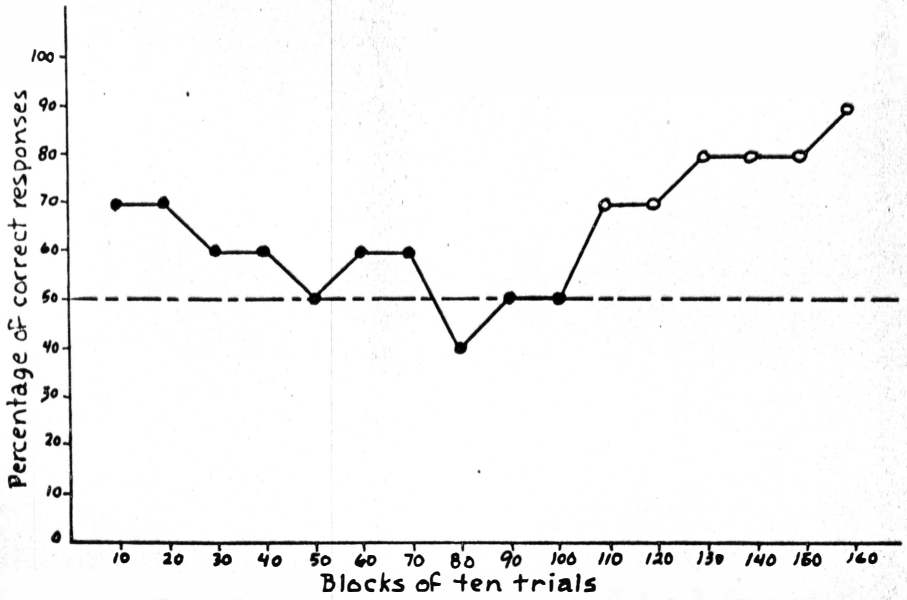


Subject 4



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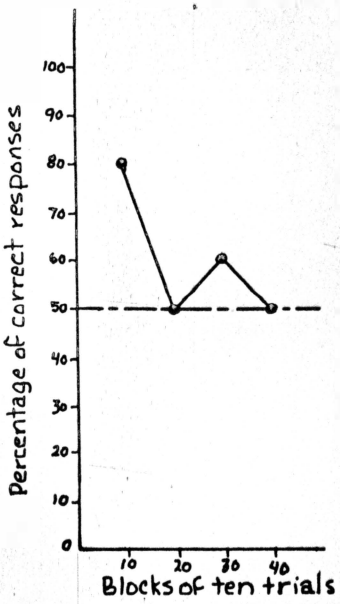

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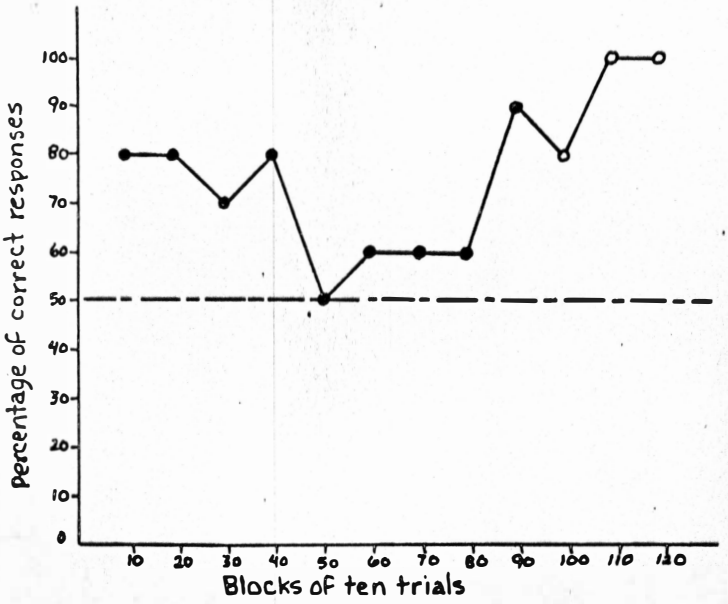
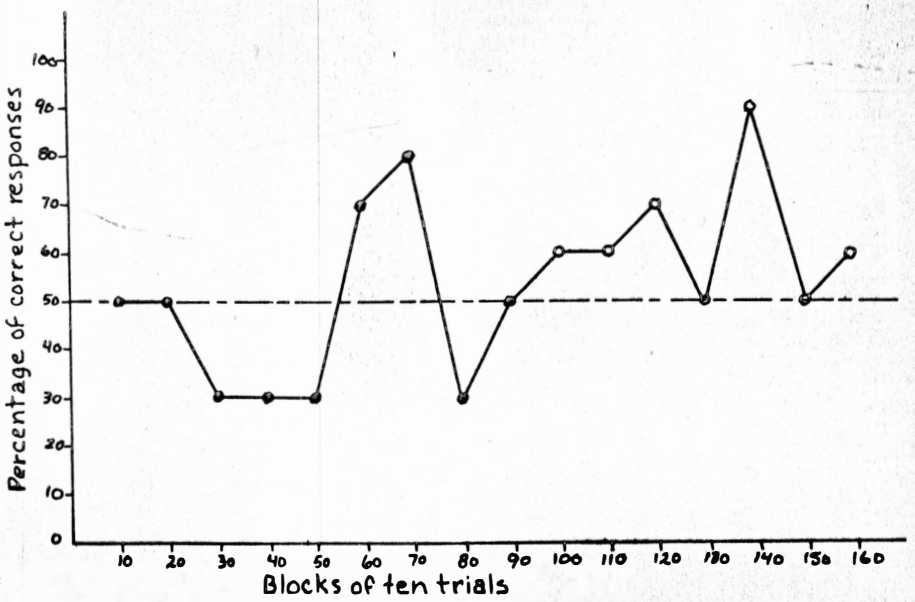
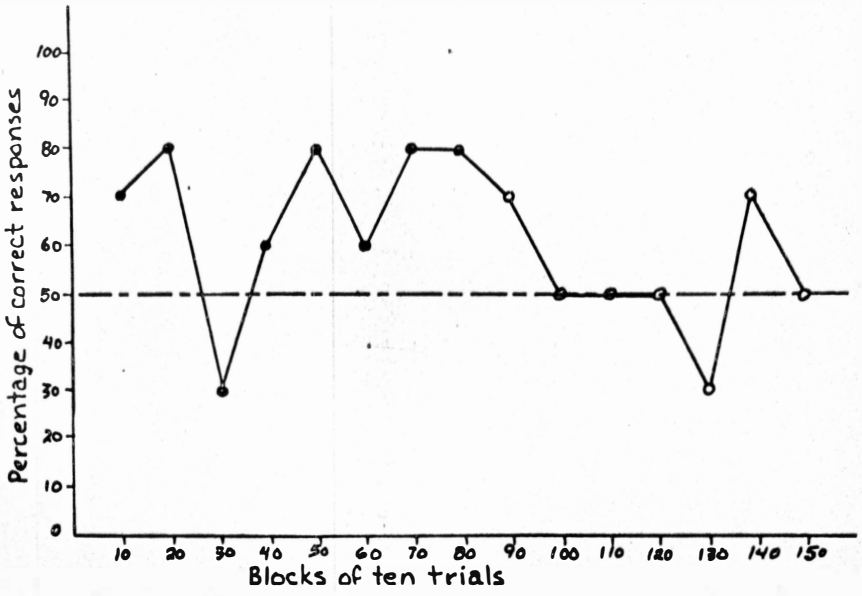


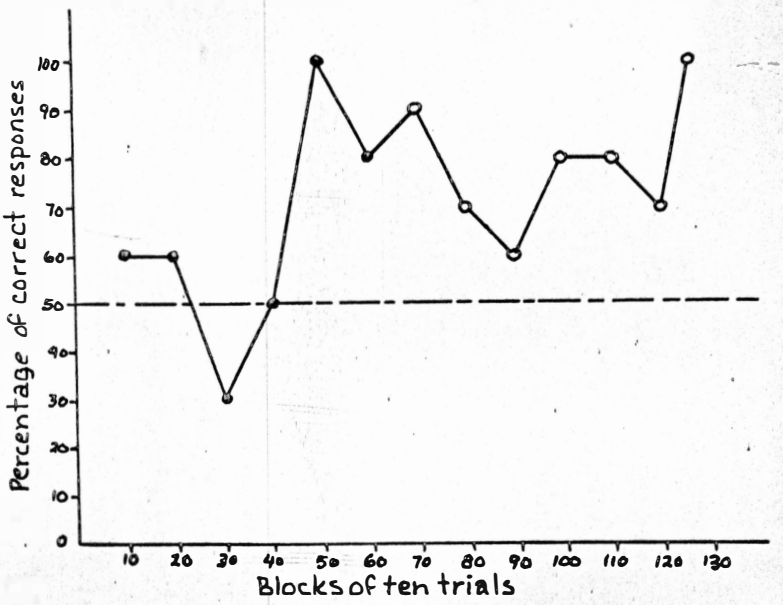
Subject 7



Subject 8



Subject 9



Subject 10

Table 3. Total percentages of correct responses of nine subjects for 75 days at two trials per day and for 97 days at one trial per day in the T-maze experiment

Subject	Two trials per day		One trial per day
	First trial	Second trial	
1	75	71	-
3	67	53	-
4	77	71	91
5	66	57	70
6	61	62	-
7	83	53	85
8	66	30	61
9	83	39	60
10	85	31	73
Total average	74	50	70

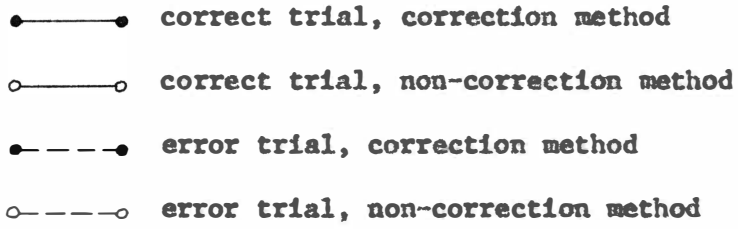
Running times for each of nine subjects are presented in fig. 11 as average times per trial for consecutive blocks of ten trials. Immediate improvements in correct response running times from the first ten trials to the second ten trials can be noted in Subjects 7, 8, 9, and 10. The times of Subjects 7 and 8 then leveled off, but those of Subjects 9 and 10 gradually increased to times above their respective initial averages. The running times of Subjects 4 and 5 remained quite constant throughout the entire T-maze experiment.

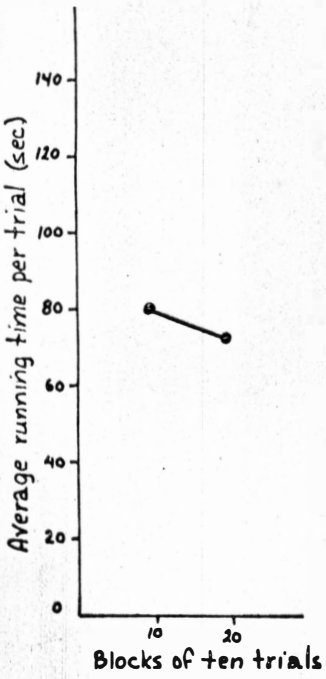
The observed paths taken by the nine subjects at the T-section (see Fig. 5) are presented in table 4. The percentage of total trials for each type of turn is given for each subject. In a total of 836 trials, 75% of the turns were made directly around a corner. Only 9% of the total turns were made by the subject crossing from one side to the opposite goal box, and of these, the subjects crossed from the incorrect to the correct side eight times more often than from the correct to the incorrect side.

There were many sheddings during the course of the T-maze experiment. Subjects 4, 5, 6, 7, and 10 each shed once, and Subjects 8 and 9 each shed twice. On the trial immediately following each of these nine sheddings, the subject made a correct response in six cases and an incorrect response in the other three cases. In three instances, the shedding was not anticipated, resulting in the subject being tested during pre-shedding period, when such testing should have been discontinued. Correct responses were made on the trial immediately prior to the "surprise" sheddings in two of the three cases.

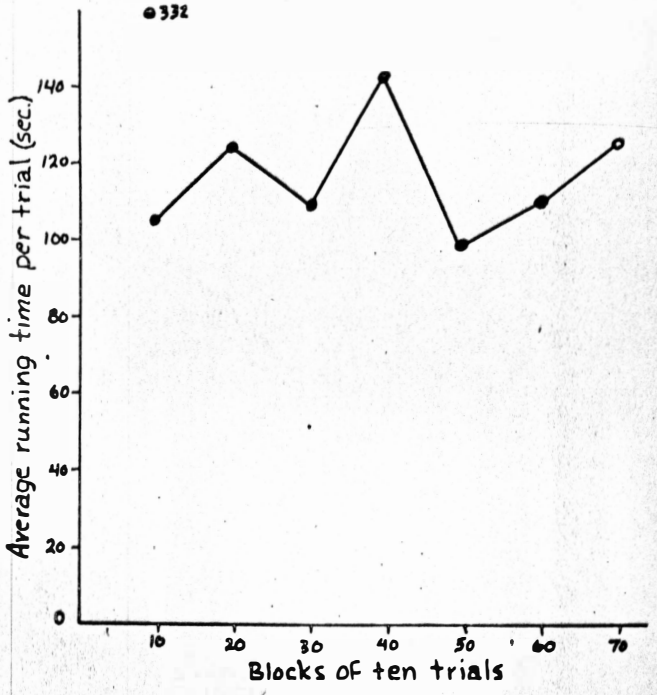
The right eye of Subject 5 became infected after that subject's 128th trial, and from that time on, Subject 5 was without the sight of that eye.

Fig. 11. Average running times per trial for each of nine subjects in T-maze experiment. (pp 34-36)

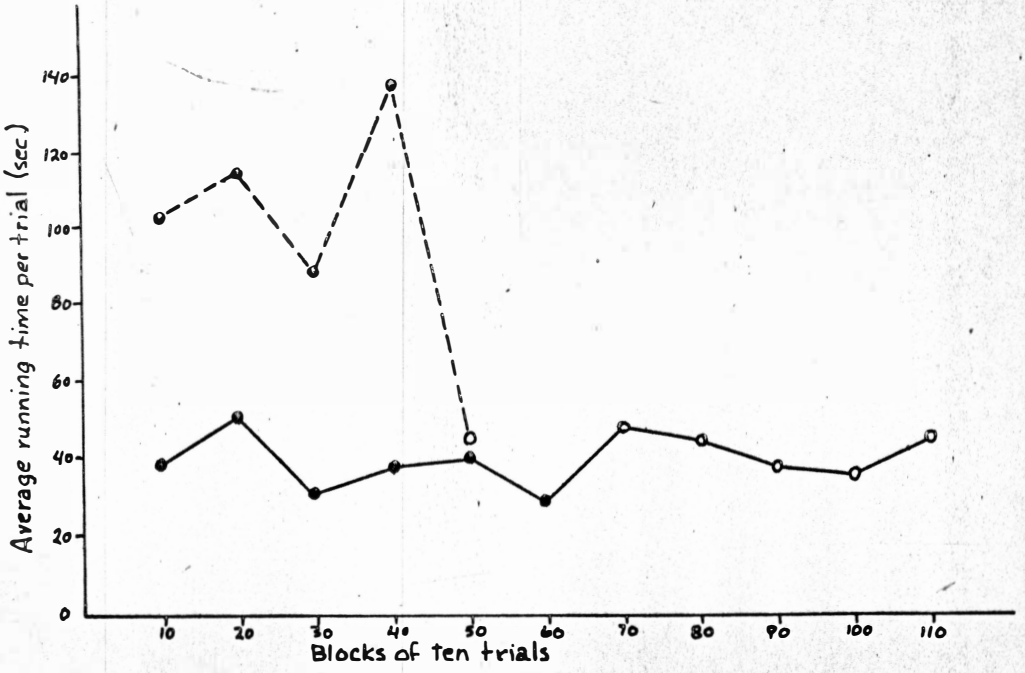




Subject 1



Subject 4



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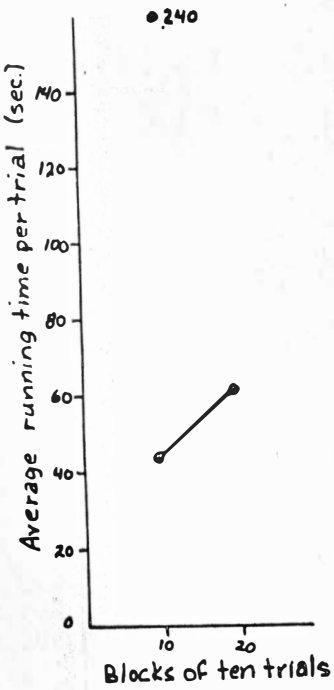

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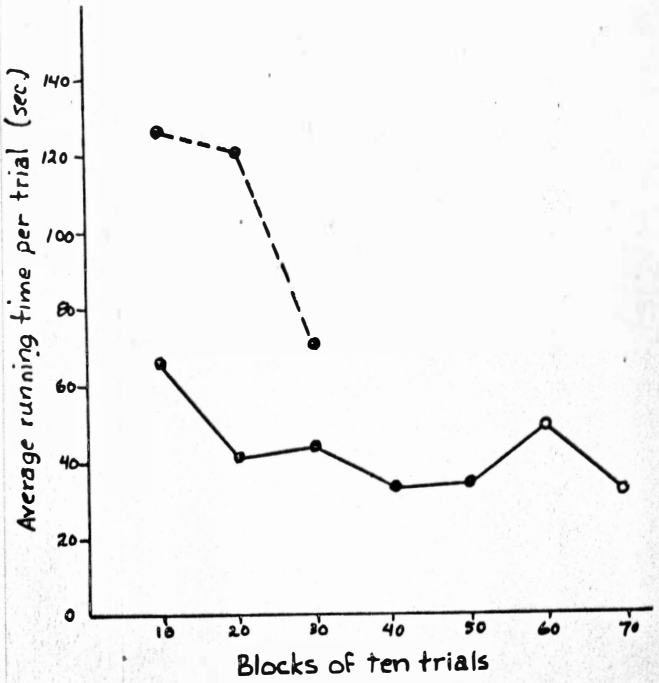
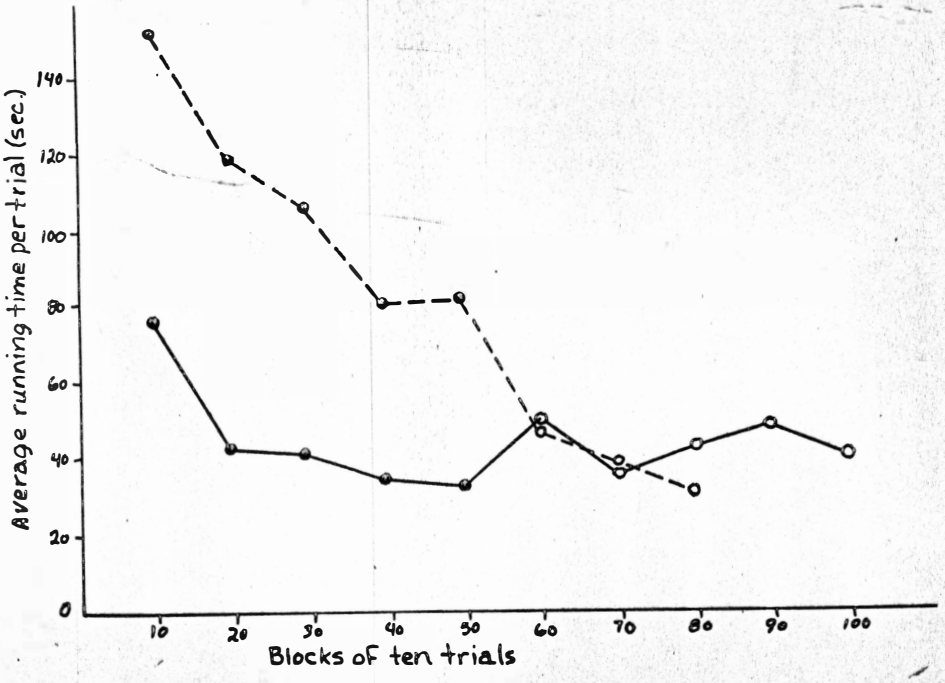


Subject 7



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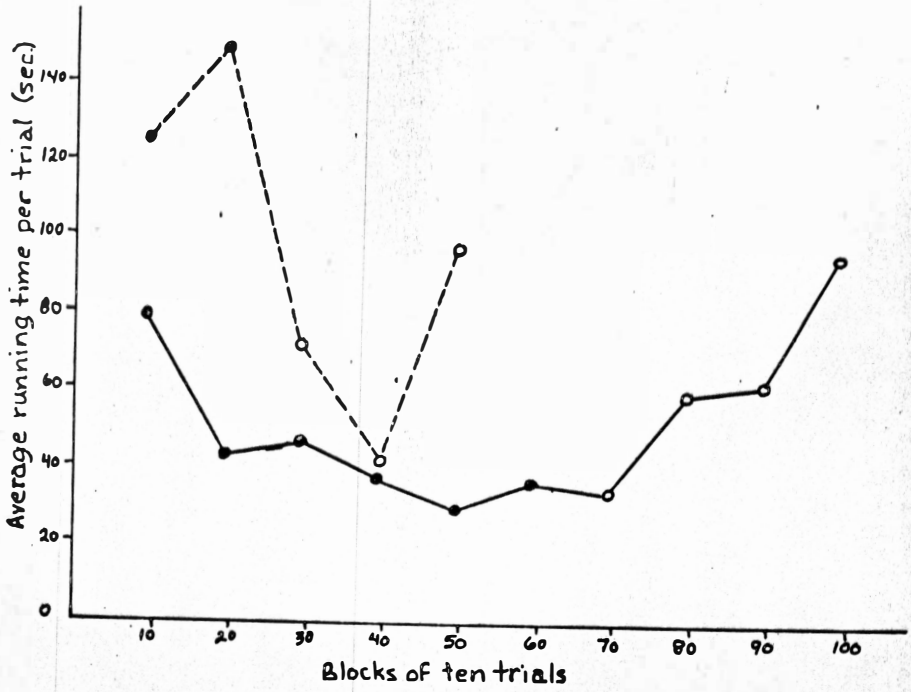

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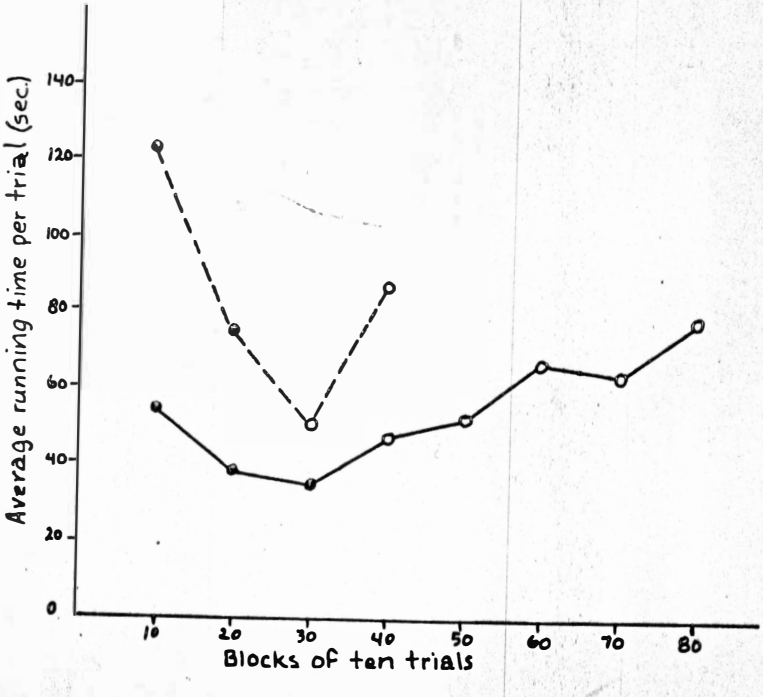
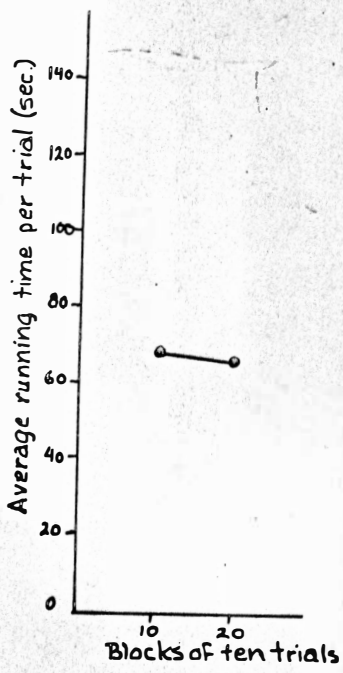


Subject 10

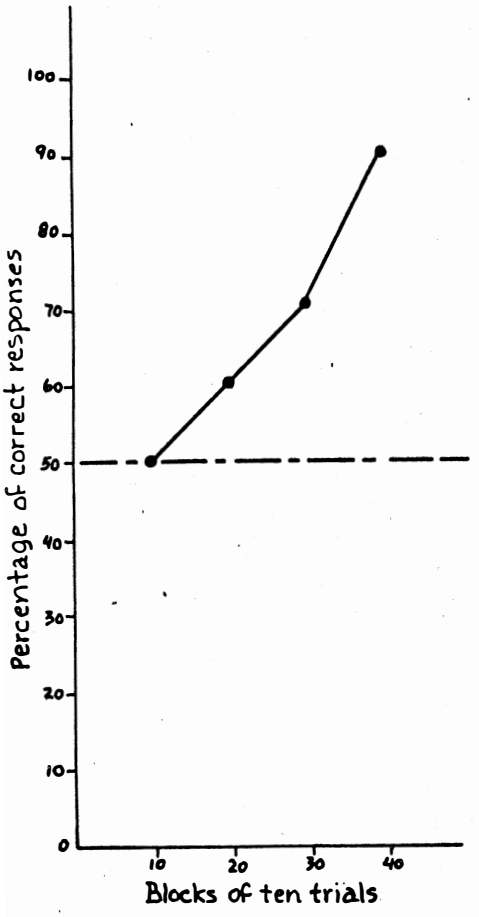


Subject 3

Table 4. General paths taken by nine subjects at T-section in the T-maze experiment (expressed as percent of total trials)

Subject	Around corner	Middle	End Wall	Across		Total trials
				Correct	Incorrect	
1	77	3	17	3	0	30
3	60	4	24	8	4	25
4	77	3	16	4	0	76
5	63	8	14	13	2	148
6	41	13	46	0	0	24
7	85	0	9	5	1	105
8	77	6	9	8	1	159
9	82	2	5	11	0	140
10	81	3	8	8	0	129
Total	75	4	12	8	1	836

Fig. 12. Percentage of correct responses in blocks of ten trials by two subjects in T-maze reversal experiment.



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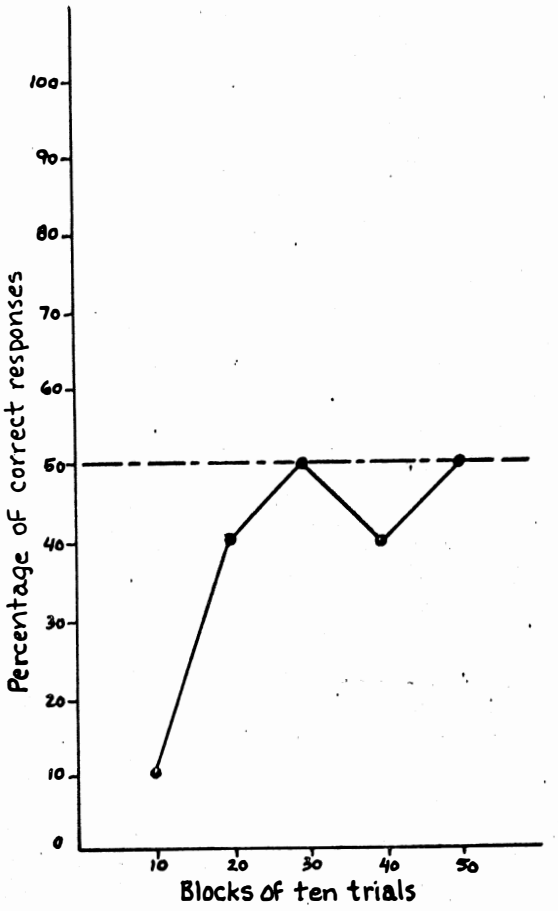
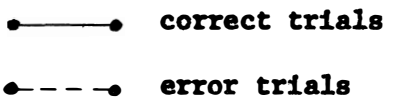
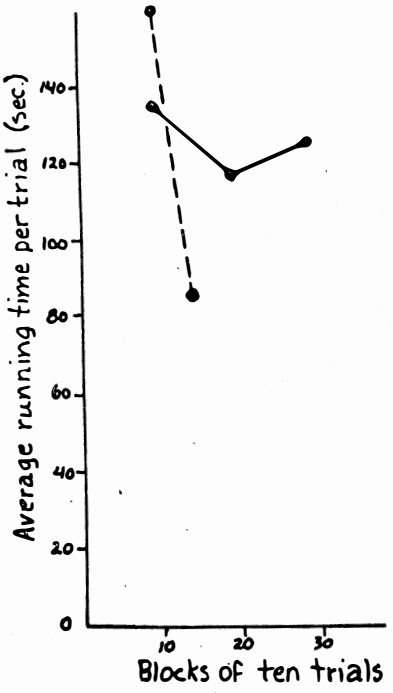


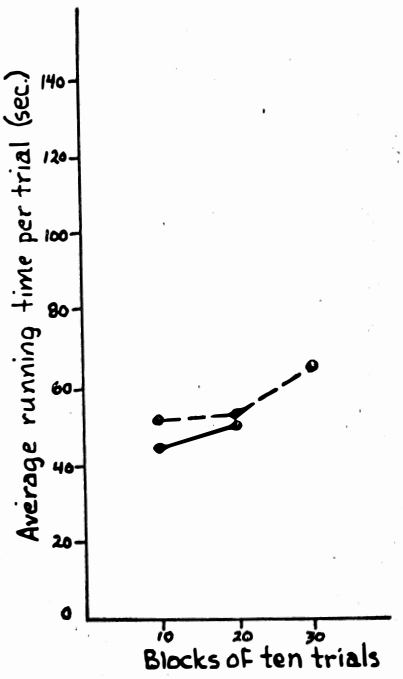
Subject 7

Fig. 13. Average running times per trial for two subjects in T-maze reversal experiment.





Subject 4



Subject 7

Table 5. General paths taken by two subjects at T-section in the T-maze reversal experiment (expressed as percent of total trials)

Subject	Around corner	Middle	End Wall	Across		Total trials
				Correct	Incorrect	
4	73	2	16	2	7	44
7	70	2	11	6	11	47
Total	72	2	13	4	9	91

DISCUSSION

When a turtle is deprived of air or a snake suddenly finds itself on an electrified grid, the animal's next response can quite safely be thought to be related to the stimulus just given. The reinforcement used in the present study, however, may be a bit less immediate. Non-experimental garter snakes were observed to readily leave their cages and go down the runway apparatus when no food reinforcement was at the other end. Initially, therefore, the subjects of this study may have been led to the food reinforcement by something else, possibly their impulse to seek hiding or escape. This impulse would have been further reinforced by the food, and it can be assumed that later the food reward was of prime importance. It is also possible that the presence of food in the goal box was detected by olfaction.

With the food reinforcement, latency times showed a general decrease and running times held steady (Figs. 6 and 7), indicating that learning was taking place. Latency times appear to be a good indicator of runway learning in snakes. Observations in this study indicate that at least two factors accounted for the irregularities in individual latency times. Most important of these was the awareness of the subject at the time the cage door was raised. If the subject was still "dozing" after the door was raised, a high latency time would result. The other factor that was noted was the location of the subject in its cage at the start of a trial. A subject at the front of its cage would naturally have a headstart on one that was behind its water dish at the rear of its cage.

Group latency and running time curves (Figs. 6 and 7) are quite similar to group results reported by Crawford and Bartlett (1966). Rather than indicating lack of acquisition, as Crawford and Bartlett concluded with their subjects, the fact that group running times leveled off can be interpreted as a positive result. Some subjects appeared only capable of reaching certain minimum times due to the amount of caution which they exhibited. The consistently low latency times of Subjects 3, 5, 7, and 8 indicate that these subjects were naturally more active, had become better habituated, or were better able to relate the opening of the cage door to the food at the end of the runway.

The change from one trial per day to two trials per day with the straight runway did not appear to affect the responses of most of the subjects. However, when subjects were tested twice per day during the T-maze experiment, a difference between results of first trials of each day and second trials of each day was noted (Table 2). It seems very improbable that a subject's hunger was less for second trials, because of the large appetites that the snakes were observed to have in the habituation period. Rather, stress seems to be the important factor, whereby if a subject was in any way traumatized during its first trial, the second trial might produce an incorrect response. In the T-maze experiment, a higher percentage of correct responses was recorded for most subjects after trials were reduced to one trial per day. The elimination of second trial responses and the normal learning which would be expected might be responsible for the improvements.

The running times of the T-maze experiment followed much of the same general trends at the running times of the runway experiment, because the movements required and the apparatus itself were essentially

the same in both experiments. Error times when the correction method was used are much higher than times for correct trials, because error times involved movement to the incorrect goal box and then to the correct goal box.

The individual times for the T-maze are not nearly as irregular as those reported by Kellogg and Pomeroy (1936), because in the latter study, subjects could make up to two errors per trial, and all times were considered together. Highly variable times were also reported by Crawford and Holmes (1966) in their attempt to condition snakes to escape a vibratory stimulus.

The increase in running times noted after 70 trials for Subject 9 and after 30 trials for Subject 10 was also apparent after 48 trials for Kellogg and Pomeroy's group of twelve subjects and after 40 trials for Crawford and Holmes' group of six subjects. It is very possible that the subjects of Crawford and Holmes were becoming habituated to the vibratory stimulus. On the basis of data and observations of the present study, no explanation can be offered for the increase in running times of Subjects 9 and 10.

In the T-maze experiment, some evidence of learning is indicated after ten trials. As shown in fig. 10, eight of nine subjects scored above 50% in their first block of ten trials. Shortly after this, the percentage of correct responses by five of these subjects (1, 3, 5, 6, and 7) dropped. Such a regression in learning was not found by Kellogg and Pomeroy (1936). A possible explanation for the regressions noted in the present study is the "correction method" that was being used. Subjects were being reinforced for incorrect turns as well as correct turns, because originally, the investigator believed that extinction of desired

responses would result if the subjects were not continually reinforced. In an attempt to curtail the regression and hasten learning, the change to a "non-correction method" was made. The change was accompanied by increased percentages of correct responses by Subjects 4, 5, and 7. The mere fact that the total number of trials given was increasing may have contributed to these correct response increases as much as the change of methods.

The amount of learning demonstrated by the group of subjects tested in the initial T-maze experiment of the present study is similar to that demonstrated by Kellogg and Pomeroy (1936). In Kellogg and Pomeroy's study, twelve subjects were tested in a double T-maze for 62-73 trials per subject, and the total number of errors made by the group decreased from about 110 within the first five trials to slightly less than 70 between trials 46 and 50, inclusive. Large differences in individual performance were noted in both studies. Results of the present study are also similar to those reported by Morlock, et al. (1968) for the ability of eastern painted turtles to learn a correct turn response in an E-shaped maze. Five of five turtles met criterion in 40-140 trials. Wolfle and Brown (1940) reported less conslusive results with a group of eleven snakes tested in a double T-maze. After 179 total trials, only 27 errorless runs had been performed in that study. Differences in methodology make reliable statistical comparisons of the four studies impossible.

In the present study, Subject 4, which learned both the T-maze and T-maze reversal exercises, appeared to be the best learner of the snakes studied, with the possible exception of Subject 1, which met criterion for the initial T-maze exercise but died before it could be tested for

reversal learning. Had there been more time available, it would have been desireable to test Subjects 5, 7, and 9 for reversal learning. Subject 7 was placed on reversal training, however, time did not permit more than 50 trials. Subsequent reversals following learning of the first reversal experiment would also have been desireable.

The movement required by the subjects of this study differs basically from that of the water snakes of Kellogg and Pomeroy (1936). Swimming in a flooded T-maze required a uniform serpentine movement. Thus, the water snakes used the entire alleyway in a regular fashion, and the point at which they arrived at a T-section would seem largely determined by its position when it left the entrance box. Kellogg and Pomeroy stated that "the constant length of previous wiggles, of which the turn was usually but a continuation, the smoothness of the turns themselves suggested chance and not anticipation or deliberation". In the T-maze and T-maze reversal experiments, the subjects often appeared deliberate in their movements and probably guided by the sense(s) of vision and/or olfaction. The tactile sense appeared to be used occasionally at corners and at the end wall. When it had reached the T-section, a subject would often move its head to face each direction. Such actions by the subjects of this study seem more indicative of a discriminative process than the primary use of the tactile sense reported by Kellogg and Pomeroy. After the loss of sight in its right eye, Subject 5 continued its trials and reached criterion for learning the T-maze. This subject had either learned to direct its movements to the right or was orienting to some cue with its left eye.

Figures in tables 3 and 4 indicate that subjects in both the T-maze and the T-maze reversal experiments stayed against one or the other of the walls of the maze during about 75% of their turns. It seems that a

certain amount of security was connected with staying near a wall. To go around the middle, to the end wall, or to cross from one side to the other means leaving that security for a short time, and therefore was done with less frequency. As indicated by the percentages in the "across" column of table 3, subjects were better able to overcome the wall-hugging tendency when there was food as a reward for making the cross. Kellogg and Pomeroy (1936) reported that most of their snakes hugged one wall or the other during most of their swimming, although no snake was ever observed to arrive at the goal box by a continuous following of one of the side walls. A wall-seeking tendency had previously been demonstrated in laboratory rats by Patrick and Laughlin (from Waters, 1937) and in three strains of Mus musculus by Fredericson (1953). In a study by R. H. Waters (1937), block-elevated multiple T-maze performance by rats was affected by a wall of the room in close proximity to one side of the maze. Results of control groups in an elevated maze equidistant from the walls of the room were not affected by the wall-seeking tendency.

It is known that during the process of shedding its skin, the snake is temporarily incapable of normal activity. Kellogg and Pomeroy (1936) reported that after each shedding, running times were high and decreased gradually until the next shedding when another increase in times occurred. Similar phenomena were noted for error data. Such disturbances were not found in this study, possibly because of differences between ecdysis in Thamnophis and ecdysis in Natrix.

More studies are still necessary to determine the learning capacity of snakes. The lack of refinements in methodology is the major block at this time. In hindsight, the present study could have been improved in a number of ways. Although the apparatus employed was basically adequate,

narrower alleyways could have, at least partially, countered the wall-hugging tendency exhibited by the snakes. More reliable results could have been obtained had the number of subjects been larger. Simultaneous testing of a control group of subjects would then have been possible. Data collected from T-maze trials of the control group could also be used as a preference test. On the basis of observations of the garter snakes used in this study, the use of experimental subjects in a preference test would very possibly result in the extinction of positive response to the runway.

According to J. M. Warren (1957), enough species at various phyletic levels have been studied for maze learning to allow for some cross-phyletic comparisons. Warren's brief survey of such studies shows that some members of the phyla Annelida, Mollusca, and Arthropoda are superior to reptiles in simple T-maze learning. Although reptiles had been shown by this time to be superior to both fish and amphibians in their ability to learn simple T-mazes, Warren states that "among the vertebrates, only mammals are clearly superior to insects with respect to maze learning". Voronin (1962) and Hinde (1970) agree that the degree of development of the organisms reflex mechanisms limit the range of tasks that can be learned. Within the vertebrates, certain tasks can be learned by most at similar rates, but other tasks are learned at varying rates at the different phyletic levels. Various vertebrates (including goldfish, tortoises, hens, rabbits, dogs, and chimpanzees) were conditioned to seek food in response to a stimulus (Voronin, 1962). Stabilization of the correct response required 4-89 trials by the goldfish and 8-25 trials by the chimpanzees. Most of the numbers of trials required by garter snakes to form a conditioned response (Table 2) fall within the ranges of trials reported for other vertebrates by Voronin. Reversal learning represents a task of greater

difficulty than learning the original response. In Voronin's study, the chimpanzees became conditioned to the reversal response in 4-6 trials, whereas the other forms tested required 25-120 trials. Voronin suggested that for the fish and tortoise, reversal learning is "a complex procedure which approximates the limit of their capacity to 'learn' in the given situation". In his study, only one of three fish and two of five tortoises reversed the conditioned response. In the present study, reversal learning was demonstrated to be within the capabilities of the garter snake. Further reversals and testing for learning of more difficult tasks are necessary before the learning capacity of snakes can be experimentally shown to differ from the learning capacities of other reptiles and other non-primate vertebrates.

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